

ECOLOGY AND BEHAVIOUR IN *PORTIA SCHULTZEI*, WITH NOTES ON RELATED SPECIES (ARANEAE, SALTICIDAE)¹

Lyn M. Forster

Otago Museum
Gt. King St.
Dunedin, New Zealand

and

Frances M. Murphy

323 Hanworth Road
Hampton, Middlesex
TW12 3EJ, England

ABSTRACT

Field observations of *Portia schultzei*, a web-building jumping spider from Kenya, Africa, reveal that it commonly inhabits the dense webs of *Ischnothele karschi*, a diplurid spider. As a detritus mimic, this spider is inconspicuous whether in a web or on the move. Laboratory studies show that it readily catches a variety of prey-spiders and insects (mainly *Drosophila*) in its own webs, in *I. karschi* and other alien webs, as well as in non-web situations. Although the basic, visually-directed, predatory sequence conforms to that of the typical salticids, several derived features, such as the extremely slow and specialised locomotory movements, long periods of immobility in a cryptic posture, the web strategies of 'quivering' and 'dropping', and shorter visual discriminatory distances (not more than 10 cm) than most other salticids, enable this spider to exploit a web environment.

INTRODUCTION

Jumping spiders (Salticidae) have long been known for their proficiency and versatility as cursorial predators (see Forster 1982a) so it has come as rather a surprise to find that some species of the genus *Portia* Karsch specialise in the use of webs to catch their prey. Web-building was first observed by one of us (FMM) in the course of rearing *P. schultzei* Karsch collected from Kilifi, Kenya, in 1974 (see Wanless 1978b, Murphy and Murphy 1983) and it was soon evident that these salticids seized insects detained by the silk. Although 'web piracy' by members of this group had been recorded several times (e.g., Gravely 1921,

¹The preparation of this paper was supported by grants from the Scientific Distribution Committee, New Zealand Lottery Board.

Bristowe 1941) the fact that some of them also build their own three-dimensional structures in which to lurk was unknown until that time. These same studies confirmed that other spiders too were acceptable prey items and explained why *P. schultzi* were frequently found in the dense, extensive webs of *Ischnothele karschi* (Bosenberg and Lenz), a diplurid spider.

The discovery that *P. schultzi* construct and utilise their own webs as well as invading those of other spiders in the pursuit of prey raises a number of questions. How is prey detected, for instance, and do these salticids rely on vision to the same extent as cursorial species? Do they behave like other members of the family, or genus for that matter, and what are the advantages of this life style to them? To investigate these questions, live *P. schultzi* were sent to LMF in New Zealand and the present paper is the result of the collaborative studies thus undertaken.

At much the same time, another series of investigations (Jackson and Blest 1982a, b) was begun in Australia, the subjects being *Portia fimbriata* (Doleschall) which had been located in northern Queensland. Some of these studies paralleled ours thus enabling us to make comparisons between the two species. Other *Portia* spp. were observed and tested by FMM and these findings also provide useful comparisons.

MATERIAL AND METHODS

Portia schultzi is a medium-sized salticid with a body length of about 7-8 mm. Its long legs are quite slender but this is seen only in the two terminal segments where the long, variously colored hairs covering the rest of the body are lacking. Fringes and tufts on certain parts of the legs supplement this hairy covering, and the many hues create a mottled effect.

Portia schultzi range from the Forest of Gedi, near Malindi, Kenya, in the north, to Durban, South Africa, in the south, and westwards to the Rift Valley. This species has also been recorded from West Africa and Madagascar. For more detailed descriptions and distribution of *P. schultzi* and other *Portia* spp. see Wanless (1978b) and Murphy and Murphy (1983).

Portia schultzi used in these studies were observed in their natural habitats in Kilifi on the coast of Kenya from the Forest of Gedi to the Shimba Hills during the following periods: 11-16 Aug. 1974; 29 Aug. - 24 Sept. 1977; 8 Aug. - 11 Sept. 1980. Spiders were located in a number of sites, viz., in the webs of *Ischnothele karschi* (most commonly), on tree trunks and the walls of buildings, in leaf litter and a stick pile, under a water container, in an old Cyrtophora web, in a tangle of pholcid and uloborid webbery, and in their own webs.

Captive *P. schultzi* were housed in variously sized plastic containers (small, 4-5 cm in diam. x 2-5 cm high; medium, 5-10 cm in diam. x 5-10 cm high; large, 10-20 cm in diam. x 15.25 cm high), with one or more corked openings, usually supplied with moist cotton wool, and kept in room conditions (15-25°C).

Some of the tests with *P. schultzi* reported here were carried out in Kilifi but most of the longer-term observations and experiments were undertaken in England and New Zealand.

Investigations included: utilisation of silk and construction of webs, behaviour in various alien webs with or without other intruders, prey preferences, as well

as the sequence of predatory reactions in web and non-web situations. In these latter tests, attention was paid to the primary events and secondary subdivisions established for *Trite auricoma* (Urquhart) and other salticid species (Forster 1977a). Briefly, these are:

- Orientation: Alert (spider adopts a 'watchful' posture)
 - Swivel (spider turns to face source of movement)
 - Alignment (abdomen lines up with cephalothorax)
- Pursuit: Walk (slow movement towards target)
 - Run (rapid movement towards target)
 - Stalk (very slow movement with lowered profile towards target)
- Capture: Pre-crouch (low profile, 2 front pairs of legs forwards)
 - Crouch (low profile, 3 pairs of legs forwards, hind legs tensed)
 - Jump (leap towards target)

A variety of prey (see 'Prey preferences') was offered to *P. schultzii* in small, medium or large containers, in web and non-web situations.

Small (3-4 mm) lures (plasticene ball, tufts of cotton wool, bits of twig and leaf) attached to clear nylon thread were moved about in the vicinity of *P. schultzii* and their reactions observed. Other events were recorded and described. More details of methods are given in text where necessary.

RESULTS

The variegated coloration and patterning of *P. schultzii* together with its characteristic 'folded legs' resting posture (Fig. 1) combine to disguise the identity of this spider in the web where, as an effective detritus mimic, it is almost indistinguishable amongst the tiny bits of bark, seeds, dust and leaf fragments which readily accumulate there. On the move on tree trunks, *P. schultzii* is all but invisible and since, in the wild, it is most likely to commute between webs via trees and shrubs, its crypticity is obviously designed to cope with the two most likely situations in which it may find itself.

Distribution and Ecology.—The marked propensity of *P. schultzii* to inhabit the webs of *I. karschi* probably means that the distribution of these two species is closely linked. *Ischnothele karschi* have apparently benefited from the modification of tropical rain forests by man since their webs are very abundant in the partly cleared secondary bush which forms most of the gardens in Kilifi, whereas they are far less abundant in the tropical rain Forest of Gedi. Perhaps this has been advantageous for *P. schultzii*, too.

Ischnothele karschi is a medium-sized diplurid (about 15 mm in body length) which builds an extensive sheet web, occasionally on the ground, but more commonly in shrubs at a height of about one metre above the ground. The dense, central region of this web becomes greatly cluttered with plant debris thus providing an apparent refuge not only for immature *I. karschi*, but also for a great variety of spiders and insects, e.g. mysmenids (most common), scytodids, palpimanids, prodidomids, pisaurids, mimetids, *Ctenus* sp., *Orchestina* sp., *Argyrodes* sp., *Cylobellus* sp., *Cosmophasis* sp., *Myrmarachne* sp., in two instances *Thyeni inflata* females with eggsacs (constructed between leaves supported in the upper threads), and once an *Olios* exuviae, as well as insects such as thysanurids, crickets and ants. Unfortunately, it was rarely possible to see



Fig. 1.—Often observed hanging motionless in its web for long periods of time, *Portia schultzi* bears little resemblance to a spider. Its long legs are tucked against the body and are thereby concealed, a mimetic attitude of the kind described by Robinson (1969). But if it sights likely prey, the legs unfold and *Portia* begins a slow stealthy trek towards it.

what parts of the web *P. schultzi* usually occupied, or how they behaved therein, although they could sometimes be seen wandering about on the periphery of the web.

Fortuitously, an *I. karschi* web built in a fold of the trunk of a baobab tree (*Adansonia digitata*) had not accumulated any fallen leaves or other debris and it was possible to see further into the interior than usual. On three successive days, a small *P. schultzi* was seen in the web but on the fourth day, three were seen at much the same time. Two days later, a half-grown *Portia* as well as a smaller one (alongside what was presumed to be its exuviae) were present although they quickly vanished into the depths of the web. None was seen during occasional observations over the next two weeks but when the web was demolished only one half-grown *Portia* was revealed although there were several small mysmenids, some thysanurids, as well as the resident owner.

These observations suggest that *P. schultzi* is nomadic, wandering from one web to another, whereas *P. fimbriata* is relatively sedentary (Jackson and Blest 1982a) and in any case, can move readily from one host web to another because of their contiguity. Evidently *P. schultzi* prefer *I. karschi* webs, since they were never found in the quite prevalent *Stegodyphus* webs and only occasionally in pholcid or uloborid webs. Moreover, they were found in widely varying non-web situations which suggests they were merely seeking for webs to invade.

A diplurid web usually harboured a single *Portia* at a time although very small spiders were sometimes found together. Moreover, a survey of about 25 webs in the Kilifi area showed that the overall distribution of *P. schultzi* was about one

individual to every third diplurid web. In one instance, a rolled-up leaf, hung in the upper strands of an *I. karschi* web, yielded a cluster of newly hatched *Portia* spiderlings. Since the hair tufts did not appear until the third instar, spiderlings were not immediately recognisable as *P. schultzei* offspring. Interestingly, Jackson and Blest (1982a) report that *P. fimbriata* females construct special webs (Type 2) prior to the suspension of suitable leaves where the eggsacs are deposited.

Behaviour in 'captive' alien webs.—*Portia schultzei*. In captivity, a *P. schultzei*, introduced into a small cage where thick webbing had been constructed by an *I. karschi*, disappeared within the hour and was not seen again, apparently a victim of the owner. It was a similar story with *Stegodyphus* sp. although the *Portia* survived for several days before vanishing. However, in a large cage where *I. karschi* had built a thick webbing extending from a retreat of dead leaves bound with silk, the introduction of a half-grown *P. schultzei*, three mysmenids, and later a number of *I. karschi* spiderlings, led to rather different results.

Although one of the mysmenids lasted for about 4 months, two disappeared within a week, and not long after, *P. schultzei* was seen to catch a young *I. karschi* on the edge of the web. Two days later, fruitflies were put into the cage whereupon the adult *I. karschi* emerged and took two, ignoring both *Portia* and the spiderlings. Indeed, *I. karschi* was never seen to attack the spiderlings although they were sometimes seen eating each other. *Portia*, however, often seized wandering spiderlings.

Initially, *P. schultzei* remained near the floor of the cage at the opposite end to *I. karschi* and generally ignored fruitflies in favour of spiderlings. After about a month it moved up to the corked opening where the fruitflies were introduced and subsequently took fruitflies as prey although there were still several spiderlings available. Then, after 3 weeks, it moulted, moved back to the bottom of the cage, and shortly afterwards disappeared, evidently a victim itself.

***Portia labiata* (Thorell):** In 1979, three *P. labiata* were collected in Malaya. One female, taken back alive to England, made a small sheet web on the underside of its cage but did not respond to fruitflies dropped into the web as *P. schultzei* had done. After being introduced into a medium-sized cage where an immature *Tegenaria* had built a retreat and a web, *P. labiata* soon seized the *Tegenaria*. Returned to its home cage, *P. labiata* was later observed hanging from the web by its 3rd and 4th pairs of legs devouring its victim, a posture usually adopted by *P. schultzei* when eating prey. In a pholcid web, *P. labiata* showed its ability to move through the threads without alerting the pholcid but although it jumped into the web after fruitflies did not succeed in catching any.

When *P. labiata* was placed on a wooden frame supporting a *Meta* web and spider, it suddenly stirred after a long period of inaction and swivelled very slowly through 30° towards the motionless *Meta* about 3 cm away. Aligning its abdomen, *Portia* slowly stalked the *Meta* along the frame, finally crouching and leaping at it from about 1 cm. After jumping back to the frame *Portia* began feeding. *Phiale* is another salticid which attacks the spider *Argiope argentata* (Fabricius) from outside the web although both victim and quarry then drop to the ground (Robinson and Valerio 1977).

When a plasticine lure was jiggled briefly to one side of *P. labiata*, it swivelled very slowly through about 40°, aligned its abdomen, then began to creep slowly, almost imperceptibly towards the now stationary lure until the side of the clear

plastic arena was reached. It did not jump but other salticids often refuse to jump at lures or live prey when barriers of glass or plastic intervene (Forster 1979b).

***Portia durbanii* Peckham and Peckham:** Not all *Portia* species make webs. A juvenile *P. durbanii* from South Africa (see Wanless 1978b) was reared by FMM through several moults and showed no sign of web-spinning activity. Fed mostly on fruitflies, it caught prey in typical salticid fashion, albeit much more slowly. This species moults in the open.

Utilisation of silk by *Portia schultzei*.—When moving about in the open or leaping across gaps, *P. schultzei* laid down a dragline and attached it at various points, as all typical salticids do. But once a number of aerial threads had been established, this salticid showed a pronounced tendency to use these threads for passage and this, in turn, increased the aggregation of aerial lines which readily became attached to each other where they crossed. However, typical salticids seldom use draglines in this manner nor do their silk threads adhere to each other in such a way. Clearly, these modifications are fundamental to the life style exhibited by *P. schultzei*.

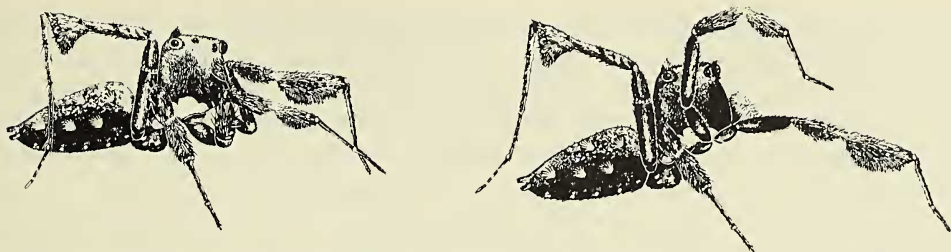
When caged, *P. schultzei* immediately constructed a few aerial threads from which it hung, upside-down. More silk was added to the preliminary structure from time to time, resulting in a three-dimensional network supporting a recognisable platform beneath which the spider usually rested. Mature males, however, seldom built such platforms; indeed, their webs were much flimsier than either female or juvenile structures.

In a web, whether its own or that of a host, *P. schultzei* almost always moved about in a languid manner interspersing stepping movements with flexing and stretching motions of the limbs, thus creating the impression of a 'lolloping' gait (Figs. 2-3). This gait is strongly reminiscent of the locomotory activity of gradungulid spiders (LMF. pers. obs.) which flex and stretch their long legs in like manner as they move about the substrate. Perhaps the flexing, stretching components of stepping actions in *P. schultzei* are necessary to manoeuvre the extra length of the limbs while keeping the body close to the ground given that 'long leggedness' is a useful adaptation in web environments.

Lolloping movements differed little regardless of whether the spider was approaching prey, exploring a new web, or walking along a substrate, although in the first situation, a directional element was present. However, lolloping seemed more pronounced during stalking than during walking or running but perhaps this was merely a function of the distance of the forward motion involved.

During the day, *Portia* remained quiescent for long periods, usually suspended upside-down from its platform, or alternatively it sought a 'vantage' point from which it apparently monitored activity in the web. For example, several captive spiders regularly sat on cork plugs all day, facing the web, never moving from there unless prey was introduced. If disturbed, their palps undulated rapidly. Another jumping spider, *Euophrys parvula* Bryant, which sits for long periods on the walls of houses keeping a 'watchful eye' on its visual territory, also undulates its palps rapidly in the presence of intruders (Forster and Forster 1973).

Without fail, *P. schultzei* returned to their platforms at night. In one instance, a spider devouring prey in a cage without a web, promptly constructed a web at dusk (holding the prey meanwhile) and then continued its meal. This nightly



Figs. 2-3.—The 'lolloping' gait of *Portia schultzii* is apparently achieved by the long legs which alternately (Fig. 2) flex and (Fig. 3) stretch as the spider makes its unhurried way towards the target.

behaviour is clearly analogous to that of many salticids which usually either make new retreats at dusk or return to an old one.

Moulting.—*Portia schultzii* exuviae were observed on some occasions either hanging in their own webs or in those of *I. karschi* thus leading to the assumption that these salticids moult in the open (also see Jackson and Blest 1982a). On one occasion, the final stage of the moult of a caged spider was observed. The moult skin was suspended in the web, attached to a thread by the claws of a fourth leg; the spider, free except for its spinnerets, was hanging from the moult skin, its pale, translucent legs still extended against the underside of the body. Some slight flexing of the limbs was noticed and then suddenly the spider began to 'twirl.' For at least 90 seconds both spider and skin 'twirled', a relatively slow motion in which both were clearly visible. When the action ceased, the spider was seen to be free of its exuviae and the legs in more normal positions. The spider darkened up quickly and some time later it had assumed its typical hanging posture in the web (see Fig. 1). Was this a freak happening or might twirling be an adaptive feature of moulting to aid the spider in casting off its skin in the open?

PREDATORY EVENTS

Predatory events were examined in four different situations (see Methods): in two cages *P. schultzii* were in their own webs and in two they were without webs.

Typical and modified salticid responses.—*Portia schultzii*'s primary responses (Orientation, Pursuit and Capture) to prey were identical in form and sequence in both the web and non-web situations to those of typical salticids but the secondary components were frequently modified. Orientation (Alert, Swivel and Alignment) always preceded approach although there was a marked tendency for small-angle ($<30^\circ$) swivels to be quite fast and for large-angle ($>30^\circ$) swivels to be abnormally slow. This suggests a distinction in the rate at which turning is mediated either between the two pairs of lateral eyes or between the principal and lateral eyes, a difference not recorded in other members of the family. However, within the visual range of the principal eyes, a series of 'tantalus-like' turns (see Land 1971) often occurred, such reactions being common to typical salticids. The rate of alignment was typical, a movement probably also mediated by the principal eyes.

During approach to the target, *P. schultzii* walked, very occasionally ran, and crept towards the target. Unlike typical salticids, however, walking along a

substrate or negotiating the web network was punctuated by leg stretching and flexing movements (lolloping) (Figs. 2-3) which tended to further reduce the already slow rate of stepping. Nor did stalking result in the low profile adopted by most other salticids (Forster 1977a) but no doubt *Portia*'s long legs precluded this posture on the ground and it would have had little value in the web. Moreover, the pursuit of a target, however prolonged, was always linear, *Portia* apparently being unable to diverge from a straight path unlike, e.g. *Phidippus* (Hill 1979). If, for instance, a fruitfly or prey spider walked consistently around the perimeter of a circular cage, *Portia* never walked around after it, although it would swivel from time to time. This behavioural limitation is also demonstrated by *Trite planiceps* Simon when its anterior-lateral eyes are occluded (Forster 1979a); under such conditions this salticid also creeps very slowly and only in a straight line towards the target, whereas normally it could give chase at speed in any direction regardless of the inconsistency of the quarry's movements (Forster 1979b). The consequences of this is demonstrated by the following test:

When *P. schultzei* and *Trite auricoma* were each presented simultaneously with a fruitfly in small identical containers, *T. auricoma* seized its quarry in 15 seconds whereas *Portia* did not succeed for 1½ hours. There were, in fact, only two circumstances whereby *Portia* could catch the fruitfly. Either the fruitfly had to remain motionless long enough for *Portia* to stalk it directly or it had to fly between *Portia*'s front legs. In brief, *Portia* cannot maintain visual contact with swift, erratically-moving prey nor can it run after it, whereas *T. auricoma* possesses both capabilities, functions most likely mediated by the anterior-lateral eyes (see Forster 1979a).

To complete the hunting sequence, *P. schultzei* halted at a critical distance from the target, usually 1.0 to 1.5 cm, placed the first two pairs of legs forward (pre-crouch) and then brought the third pair up (crouch), as typical salticids do (see Forster 1977a), before lunging forward and seizing its quarry. Generally, the 4th pair of legs did not leave the ground, or the web, so that, in effect, the spider simply reached forward to grasp its prey. Nonetheless, in escape situations, these spiders were able to move very fast and often jumped distances of several centimetres during which the 4th pair of legs clearly left the ground.

Atypical tactics.—One tactic by which prey was seized has not been recorded previously in salticids, as far as we know, although there are similarities to the behaviour of *Phiale* (q.v.). A prey spider that ran beneath *Portia*, alert in its web, could be captured when *Portia* dropped on it from distances of up to 8 cm above it. The "drop", always with *Portia* in a web, was extremely rapid so that details of the movement could not be recorded by eye. If *Portia* missed the target, it quickly hauled itself back to the original look-out site in the web and waited for another attempt. Moreover, it usually positioned itself as before which is exactly what Hill (1979) found in *Phidippus pulcherrimus* Keyserling when testing this spider's capacity for re-orientation on a substrate after jumping at prey in mid-air. Clearly, too, *Portia* was alert for a second chance, for it could be seen swivelling in the web as the object of its intentions moved about below it. Normally, a subsequent drop was successful. However, dropping was a more common occurrence from 2-4 cm above, regardless of whether the target was in the web or on the ground, because longer drops were generally inhibited by web structure. We never saw *Portia* attempt a drop if there was even the flimsiest of

silk structures between it and the target so we presume that the spider can determine the presence of silk by sight. If, in the wild, *P. schultzii* lurked in the lower portions of a web, it would be able to drop on insects and spiders moving about on the ground below but such behaviour has not been observed.

A second web stratagem, not seen in typical salticids, was recorded as a 'quiver.' *Portia schultzii* always crept very, very slowly towards motionless prey, especially if it was roughly equal in size to or larger than itself. When within about 2-3 cm of its quarry, *Portia* might pause for up to 10 minutes, but in one case for 25 minutes, during which time the body would quiver with very rapid motions at fairly regular intervals. This movement was transmitted to the web and hence to the target. It is difficult to say, unless one has seen both performances, whether quivering is comparable to web vibration and tweaking in *P. fimbriata* (Jackson and Blest 1982a) although it seems as if, in *P. fimbriata*, these agitations of the web were caused by movements of the limbs whereas in *P. schultzii* the entire body appeared to be involved. We never saw *P. schultzii* tweak the web as these authors described for *P. fimbriata*. In almost all instances, the quarry had remained completely motionless during the approach by *Portia* so it seems most likely that quivering was designed either to enhance some aspect of the spider's visual perception of the target or to induce its movement.

Distances at which prey is detected.—In large, domed terraria, *P. schultzii* constructed extensive but not dense networks of silk in the upper half of the dome and mostly placed their platforms near the centre. From here, and the side of the dome where they often sat, *Portia* had a range of vision extending some 10-15 cm across and above, with about 25 cm below.

Under illumination levels ranging from 1500 lux to bright sunlight, the distance at which prey was detected was 9 or 10 cm. No responses to prey were ever observed at distances greater than this, despite the fact that flies and spiders introduced into the cage provided ample opportunity for long distance perception and recognition to occur. Compare this behaviour to that of *Trite auricoma*, for instance, which swivels towards a movement up to 75 cm away and approaches suitable targets from about 20 cm (Forster 1977a, 1979a). Presumably, there is little advantage to *Portia* in being alerted to prey at any great distance since its slow rate of locomotion would seem to preclude it from ever reaching the target in time to capture it. Nor was there the slightest indication that detection and prey capture were mediated by other than vision; prey trapped out of sight in the web but within 10 cm elicited not the slightest response from *Portia*.

At luminance levels of less than 100 lux, *P. schultzii* did not respond to prey but between 100 and 500 lux they detected, approached and seized prey from distances up to 6 cm. Above 500 lux response distances increased but reached a maximum of about 10 cm at 1500 lux. More precise measurements obtained from courtship and agonistic interactions (Forster, in prep.) confirmed that reliable discriminations can only be made up to 10 cm away.

Reactions to lures.—Whether in or out of the web, *P. schultzii* treated all moving lures as potential prey. Reactions included all elements of the salticid prey-catching sequence: Alert (if target in front); Swivel (if target to side or rear); Walk, Run or Stalk (depending on mobility of target); Follow (if target receding); Pre-crouch, Crouch and Lunge (if target stationary but jiggled slightly).

These tests ($n = 36$) showed that target movement was a most important stimulus parameter, apparently over-riding details of target shape and pattern,

since *P. schultzei* did not discriminate between the items used as lures and actual prey.

Other observations were as follows:

1. No reactions occurred at distances greater than 10 cm.
2. If movement of the target was erratic, *Portia* did not pursue it.
3. If the target was stationary, *schultzei*'s approach was extremely slow (5 mm/min - 100 mm/min) and very long pauses (up to 25 mins) preceded pre-crouch, crouch and lunge. In 43% of cases, the sequence was not completed.
4. If the target was stationary, but jiggled slightly (cf. 3) *Portia*'s approach was much faster and the sequence was always completed.
5. If lures were trailed directly away from *Portia*, *Portia* followed — the faster the lure receded, the faster *Portia* moved (up to a limit). *Trite planiceps* behaves in a similar fashion under such predatory conditions (Forster, 1985).

Prey preferences.—*Drosophila* were the most readily available insects hence were regularly offered to captive *P. schultzei*. The *P. schultzei* spiderlings, mentioned previously, fed readily on them and in the tests designed to identify predatory events they were seized almost as frequently as prey spiders. House flies were less likely to be caught, *Portia* invariably retreating before their sudden flights and buzzing onslaughts. If, however, a fly was left for several days in a small cage, gradually becoming less active or entangled in the web, *Portia* might eventually catch it. Although various insects were found in diplurid webs it was not possible, owing to the opacity of the webs, to say whether *Portia* ever ate any of them. But once, on a wall in Kilifi, *Portia* was seen eating a fly.

Offered one live and one dead *Drosophila*, *Portia* stalked and lunged at the dead one, although it took 5 minutes to cover the two-centimetre distance to the lunging point. Perhaps the live fly provided the initial stimulus but clearly the stimulus properties of the dead fly were able to elicit the remainder of the sequence. Moreover, there were other occasions on which *Portia* accepted dead flies although details of the seizures were not witnessed. Hence movement is not the only inducement needed for stalking and lunging.

Thomisids offered as prey when *P. schultzei* was off the web were rarely captured, largely because these prey-spiders had a tendency to wave their front pairs of legs at any 'menacing object', a ploy which certainly deterred *Portia*. However, on two occasions, when *Portia* was in a web and a thomisid was moving about on the ground several centimetres below, *Portia* dropped and scooped it up. Theridiids, too, were often caught by this tactic, generally when both prey and predator were in the web.

Small jumping spiders (unidentified) were only caught when both were on the ground but capture depended on these prey-spiders either (i) remaining stationary long enough for *Portia* to stalk them directly or (ii) walking away from *Portia* in a straight line. This type of departure apparently induced *Portia* to follow in much the same way as some male salticids follow a mate (Forster 1977c).

The ready availability of *Cambridgea* sp. meant that they were offered to *P. schultzei* more frequently than other prey spiders. All the tactics at *Portia*'s disposal were used against them but since *Cambridgea* tended to remain motionless for long periods of time, very slow approaches were customary and body quivers were commonly employed.

Araneids were more likely to be captured if they moved about. *Portia* regularly stalked the motionless spiders but if unable to induce movements by quivering,

or to obtain adequate stimulation by sidling around and scrutinising the araneid from different angles, *Portia* would abandon the hunt.

Given a choice off the web between active prey (fruitflies, small salticids, thomisids, *Neoramia* spp.) and relatively quiescent prey (*Cambridgea* spp., *Araneus* spp.), *Portia* invariably selected the laggards, stalking very slowly and lunging only when its quarry stirred slightly.

DISCUSSION

Our observations show that *Portia schultzii* is primarily a web-dweller and that the web it occupies may be of its own construction or that of an alien species. Within the geographical limits of the present study, the most preferred alien web appears to be that of a diplurid spider, *Ischnothele karschi*. We find, moreover, that *P. schultzii* readily catches prey when in a web and just as readily when away from a web. As a web-dweller, therefore, the question is, does this spider catch prey in the manner of a typical salticid or does it use methods more commonly associated with other web-builders?

The evidence from this study is that *P. schultzii* is a salticid-like hunter and that it has only secondarily adapted to a web-dwelling lifestyle. This conclusion is based, first, on the fact that *P. schultzii* hunts solely by vision (also see Forster 1982a) and since the structure of the eyes is very similar to that of the typical salticid (Forster, pers. obs.) the conclusion is that the peripheral detection of prey, as evidenced by swivelling, is mediated by the lateral eyes and that the ensuing pursuit and capture of prey are mediated by the principal eyes. Second, *P. schultzii* employs the same set of predatory events as typical jumping spiders and although two web tactics (quivering and dropping) have been added to the basic salticid repertoire, both are guided by vision and neither appear to be inherited from any other web-builders. Third, *P. durbanii* is shown to be a cursorial hunter despite its known morphological relationship to the web-building *Portia* species (Wanless 1978b). Moreover, all known *Portia* species possess two claws and a claw tufts (Wanless 1978b), an acknowledged salticid feature which links them to a cursorial predecessor (Gertsch 1979). Taken together, these findings suggest that a number of *Portia* species, including *P. schultzii* have secondarily adapted to a web-building and web-invading lifestyle.

The commonality of the visually specialised hunting strategy in salticids suggests that the division of labour, which probably evolved to meet the needs of a diurnal predator (Forster 1982b), was so successful that these spiders soon outstripped their closest relatives. This basic cursorial strategy gave rise to a variety of adaptations by which salticids were able to exploit a vast array of terrestrial habitats and situations. One of the most successful of these — mimicry — has taken many forms (see Reiskind 1977, Wanless 1978a, b, Platnick 1984, Edwards 1984). *Sarinda hentzi* Banks, for example, is a Central American ant-mimicking salticid which not only has the appearance of an ant, but also spends much of its time in ant-like behaviour, being diverted only spasmodically for bouts of salticid-like predation and reproductive activities (Forster 1982a and pers. obs.). *Portia schultzii*, too, is a mimic, spending much of its time posing as a piece of bark which has fallen into a web, reacting like a salticid only when it sights potential prey or mate.

In adapting to a web environment, *P. schultzei*'s precursor retained the primary visual elements of prey capture, i.e. orientation, pursuit and capture (Forster 1977a) because these visually mediated events characterise the predatory sequence in the present-day *P. schultzei*. It was in the secondary components that adjustments were required. In a web, it was clearly advantageous for large-angle swivels to be performed slowly because fast ones might produce vibratory stimuli or visual signals that would alert a neighbouring web-dweller or the host spider. Slow, spasmodic approaches to prey would obviate the same kind of disturbances and also be more appropriate when negotiating an alien web structure. 'Dropping' onto the prey from the relative safety of a vantage point does not carry the same risk, hence rapid movement would be acceptable under these conditions.

Portia's failure to chase fast-running and erratically-moving prey either on or off the web may mean that the anterior-lateral eyes are not involved in post-detection behaviour as shown for *Trite planiceps* (Forster 1979a, 1985). Moreover, because insects are usually immobilised by the silk, or prey spiders quiescent, 'quivering' by *P. schultzei* may be an adaptive ploy by which movement is induced in the quarry and visual cues enhanced, selection processes having apparently ensured that its nature and frequency do not imitate those of a trapped insect and so attract another predator to the scene.

Portia schultzei pierces prey after lunging at it, or scoops it up after 'dropping' whereas Jackson and Blest (1982a) observed that *P. fimbriata* swoops at, stabs or picks up prey. Nevertheless, behavioural variability in *P. schultzei* does not appear to be related to diversity in the type of prey encountered as shown by *P. fimbriata* (Jackson and Blest 1982b) but rather to differences in prey mobility as well as the conditions under which predation occurs (Forster 1985). Moreover, *P. schultzei* does not 'tweak' the web as Jackson and Blest (1982a) describe for *P. fimbriata* for 'quivering', which has some similar characteristics, does not appear to have the same functions.

In captivity, *P. schultzei* catches a wide range of spiders as prey and, unlike *P. fimbriata* (Jackson and Blest 1982a), catches insect prey just as readily. *Portia labiata* exhibits a similar ability to catch prey both in its own webs as well as alien webs and is also able to jump into and out of webs, a skill not demonstrated by *P. schultzei* nor, it seems, by *P. fimbriata*, because Jackson and Blest (1982a, b) make no mention of it. Moreover, the absence of web-building in *P. durbanii* highlights the need for caution in making assumptions about the evolutionary status of this genus until more species have been studied.

Many of the behaviours exhibited by known *Portia* species have been observed independently in cursorial salticids. For example, a New Zealand *Marpissa* sp. has been seen hunting on an araneid web (Forster, pers. obs.). An unidentified salticid has been observed devouring ants while suspended from a thread, and *Phiale* apparently makes a practice of leaping onto *Argiope* in its orb-web (Robinson and Valerio 1977) as does *Phidippus* (Tolbert 1975). In behaviour comparable to that of *P. fimbriata* taking insects from the chelicerae of the web spider host (Jackson and Blest 1982a), an Indian *Marpissa* sp. robs ants of their prey (Marson 1947). Similar prey robbery, described as kleptoparasitism, has been reported for four Japanese salticid species, one of which has been seen devouring the eggs of another spider (It 1977). Because the behaviour of relatively

few salticid species is known, it is likely that many more diverse strategies are yet to be discovered.

ACKNOWLEDGMENTS

We would like to thank Mr. Neville Chalke for acting as a courier and bringing *Portia schultzii* to Dunedin for study.

REFERENCES

- Bristowe, W. S. 1941. The Comity of Spiders. Vol. 2. Ray Society, London.
- Edwards, G. B. 1984. Mimicry of velvet ants (Hymenoptera: Mutillidae) by jumping spiders (Araneae: Salticidae). *Peckhamia*, 2(4):46-49.
- Forster, L. M. 1977a. A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). *New Zealand J. Zool.*, 4:51-62.
- Forster, L. M. 1977b. Mating behaviour in *Trite auricoma*, a New Zealand jumping spider. *Peckhamia*, 1:35-36.
- Forster, L. M. 1979a. Visual mechanisms of hunting behaviour in *Trite planiceps* — a jumping spider. *New Zealand J. Zool.*, 6:79-93.
- Forster, L. M. 1979b. Comparative aspects of the behavioural biology of New Zealand jumping spiders (Araneae: Salticidae). Ph.D. dissertation. University of Otago, New Zealand. 402 pp.
- Forster, L. M. 1982a. Vision and prey-catching strategies in jumping spiders. *Amer. Sci.*, 70(2):165-175.
- Forster, L. M. 1982b. Visual communication in jumping spiders (Salticidae). Chapter 5, *In Spider Communication: Mechanisms and Ecological Significance* (P. M. Witt and J. S. Rovner, eds.). Princeton Univ. Press, Princeton.
- Forster, L. M. 1985. Target discrimination in jumping spiders. Chapter 13, *In Neurobiology of Arachnids*. (F. Barth, ed.). Springer-Verlag, Frankfurt, Berlin.
- Forster, R. R. and L. M. Forster. 1973. New Zealand Spiders, an introduction. Collins, Auckland, London. 254 pp.
- Gertsch, W. J. 1979. *American Spiders* (2nd Edition). Van Nostrand Reinhold Coy, New York.
- Hill, D. E. 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. *Behav. Ecol. Sociobiol.*, 5:301-322.
- It, N. 1977. Observations on a strange plundering behaviour in salticid spiders. *Acta Arachnol.*, 27:209-212.
- Jackson, R. R. and A. D. Blest. 1982a. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae: Salticidae) from Queensland: utilisation of webs and predatory versatility. *J. Zool. London*, 196:255-293.
- Jackson, R. R. and A. D. Blest. 1982b. The distances at which a primitive jumping spider, *Portia fimbriata*, makes visual discriminations. *J. Exp. Biol.*, 97:441-445.
- Land, M. F. 1971. Orientation by jumping spiders in the absence of visual feedback. *J. Exp. Biol.*, 54:119-139.
- Marson, J. E. 1947. The ant mimic, *Myrmarachne platyleoides*. *J. E. Africa Nat. Hist. Soc.*, 19:62-63.
- Murphy, J. and F. Murphy. 1983. More about *Portia* (Araneae: Salticidae). *Bull. British Arachnol. Soc.*, 6(1):37-45.
- Platnick, N. I. 1984. On the pseudoscorpion-mimicking spider *Cheliferoides* (Araneae: Salticidae). *J. New York Entomol. Soc.*, 92(2):169-173.
- Reiskind, J. 1977. Ant-Mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica*, 9(1):1-8.
- Robinson, M. H. 1969. Defenses against visually hunting predators. Pp. 225-259, *In Evolutionary Biology* (T. Dobzhansky, et al., eds.), vol. 3.
- Robinson, M. H. and C. E. Valerio. 1977. Attacks on large or heavily defended prey by tropical salticid spiders. *Psyche*, 84(1):1-10.

- Tolbert, W. W. 1975. Predator avoidance behaviours and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche*, 82(1):29-52.
- Wanless, F. R. 1978a. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. *Bull. British Mus. Nat. Hist. (Zool.)*, 33(1):1-139.
- Wanless, F. R. 1978b. A revision of the spider genus *Portia* (Araneae: Salticidae). *Bull. British Mus. Nat. Hist. (Zool.)*, 34(3):83-124.

Manuscript received March, 1985, revised July 1985.